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On the Structure and Affinities of Some Cretaceous Plants from Hokkaido

Contributions to Cytology and Genetics from the Departments of Plant-Morphology and of Genetics, Botanical Institute, Faculty of Science, Tokyo Imperial University, No. 94

By

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With 4 Plates and 30 Text-Figures

In the Botanical Institute of the Tokyo Imperial University there are microscopic preparations as well as unprepared materials of fossil plants from northern parts of Japan which were collected mainly by Professor K. FUJII. Some of the preparations and some other materials cut by the writer remained undetermined. Shortly after the publication of his study on fossil tree ferns (9), the writer had, in the spring of 1928, an opportunity of visiting Europe and to study these preparations at the British Museum (Natural History) in London. The present paper contains the results mainly obtained there. Some of the preparations described here were shown at the meeting of British Association for the Advancement of Science held at Glasgow, September 1928, and also at the annual meeting of "Deutsche botanische Gesellschaft" held at Danzig, August 1929.

Yezopteris polycycloides, gen. et sp. nov.

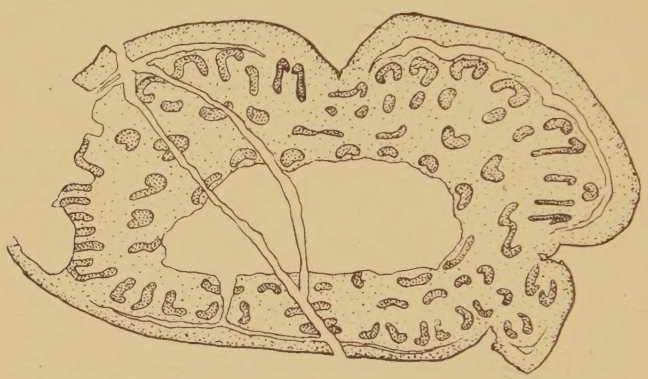
Pl. XVIII, Figs. 1–4; Text-figs. 1–4

Diagnosis

Fern petiole with no superficial appendages, circular or elliptical in cross section. Stelar system consists of three or more concentric rings, each ring consisting of U- or V-shaped meristeles, either separate or connected with one another, with the typical fern structure. In hypodermis and around each meristele is found a layer of sclerenchymatous cells.

Material

Specimen No. A. A dark-brown rod-shaped specimen, about 5 cm. in length, embedded in a nodule. In cross section (Fig. 1; Text-fig. 1) it is elliptical, 20×12 mm. in diameter, though with irregular outline owing to damage. In the center is a large hollow cavity, 7×4 mm.



Text-fig. 1. Cross section of Specimen No. A, showing the central cavity and the arrangement of meristeles. Compare Pl. XVIII, Fig. 1. (× 4)

in diameter; surrounding it are found three concentric rings of the stelar system, each ring consisting of many U- or V-shaped meristeles. Five cross sections were made.

Specimen No. B. A dark-brown rod-shaped specimen, about 9 cm. in length, also embedded in a nodule. The nodule was broken longitudinally into two, and one of the bisected pieces was used for investigation. In cross section (Fig. 3; Text-fig. 2) it is semicircular, 10 mm. in diameter, and includes the parts of three concentric stelar rings, each of which consists of U- or V-shaped meristeles. In one section we find a part of the fourth stelar ring. Five cross sections were made.

Both from Yubari, Ishikari, Hokkaido; Upper Cretaceous; found by Prof. K. Fujii in 1911, and No. A was formerly prepared by him, and No. B recently by the writer.

Internal Structure

The outer surface is smooth showing no appendages. Epidermis and hypodermis, about 5–20 cells thick, consist of small sclerenchymatous cells and pass gradually into the inner fundamental tissue consisting of parenchyma. Embedded in the fundamental tissue we find concentric stelar rings, at least three in number; the number of

Text-fig. 2. Cross section of Specimen No. B, showing the arrangement of meristeles. Compare Pl. XVIII, Fig. 3. (× 4)

Text-fig. 3. One part of Text-fig. 1 (upper right side) magnified, showing the meristeles with their tracheidal elements. Compare Pl. XVIII, Fig. 2. (× 12)

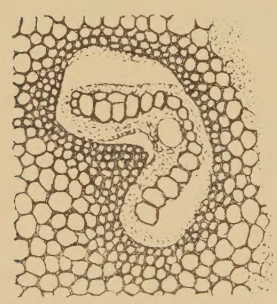
rings, however, is not certain, for No. A has a large central cavity at the inside of the third ring and No. B shows the incomplete central part (Text-figs. 1–2), but as we find a part of the fourth ring in one of the sections of No. B, it might have more than three rings. Specimen No. B seems to have no central cavity, so that the large central cavity in No. A seems to be not original but to be caused by accidence.

The form and structure of the meristeles are somewhat different at different parts of the rings (Fig. 2; Text-fig. 3); the first or outermost ring is composed properly of U-shaped meristeles with the open side directed inwards, neighbouring meristeles either connected with each other by their ends or separated into small pieces with an arc-, rod-, or V-form. The number of proper meristeles is about twenty five in No. A. The second or middle ring is simpler and smaller than the first, consisting of V-shaped meristeles, some of which are connected side by side in W- or wavy form. Both arms of each V-shaped meristele open outwards, the pointed corner being directed inwards. The number of proper meristeles is about twenty in No. A. The third or inner ring consists also of V-shaped meristeles, some of which are connected in W- or wavy form in No. A as in the second, and in No. B they are connected completely into a continuous wavy band. Each meristele or wave is similar in form to that of the second ring, but differs in that both arms of the meristele open inwards, the corner directed outwards; moreover, the curvature of the meristele or wave is not so strong as in the second. The number of proper meristeles is about fifteen in No. A.

The fourth ring which is found only in one section consists of a wavy system, the details of which, however, are uncertain.

From the successive cross sections it is quite certain that neighbouring meristeles in one and the same ring separate into small pieces or connect with each other by their ends in wavy form, but their separation and connection take place over so long a distance that we can only find such processes in a few meristeles. The connection of the meristeles in different rings is not observed.

In all cases, surrounding the meristele is a sheath of sclerenchymatous cells, several layers thick (Fig. 4; Text-fig. 4), which makes it easy to distinguish the meristele from the fundamental tissue. The preservation of the meristele is not good, only xylem elements, naturally tracheids, being preserved, though not complete. They are arranged nearly in one row, rarely in two, and the smaller ones representing the protoxylem are situated on the corner of the curved meristele, sometimes accompanying a small cavity, the protoxylem cavity, in front of it; these features agree with the meristele of the petiole of some living ferns, especially of Polypodiaceae and Cyatheaceae.



Text-fig. 4. One of the small meristeles well preserved, showing the arrangement of tracheids, the protoxylem cavity, and the thick-walled cells around the meristele. Compare Pl. XVIII, Fig. 4. (× 50)

Affinity

Judging from the features above given it is certain that this fossil belongs to a fern; besides, there is no doubt that this is the petiole of a rather large fern, as it has no external appendages and has characteristic structure of the vascular bundle.

The most important and characteristic point of this fern lies in its possessing a polycyclic stelar system. The ferns whose stems have polycylic steles are Marattiaceae, Matoniaceae, Cyatheaceae, some Polypodiaceae and Psaroniaceae, of which the last is similar to the present fern though quite different in stelar arrangement. The fern petioles with polycyclic steles belong to Marattiaceae, Cyatheaceae and some Polypodiaceae, all of which have, however, quite different types from the present fossil. Thus, the fern now in discussion is quite different from the fern stems or petioles hitherto known, and may be

a new petiole. But we have no definite ground in inferring to what group of ferns the present species should belong. We might say, though without confidence, that the present fossil has a relationship to the Cyatheaceae in having a complex stelar arrangement, though of a different type, and a similar structure both of the meristele and fundamental tissue. Perhaps, this is a representative of a new family of the Filicales which would be ranked near the Cyatheaceae. The generic name given is derived from Yezo, the old name of Hokkaido, and the specific name from its peculiar stelar system.

Solenostelopteris loxsomoides, sp. nov.

Pl. XVIII, Figs. 5–7; Text-figs. 5–7

Diagnosis

Fern stem or rhizome, elliptical in cross section, with superficial conical multicellular hairs. The stele is solenostelic, elliptical in cross section, either continuous in a ring or interrupted by leaf gap. Fundamental tissue mainly thick-walled, outer cortex thin-walled, continuous to hair bases.

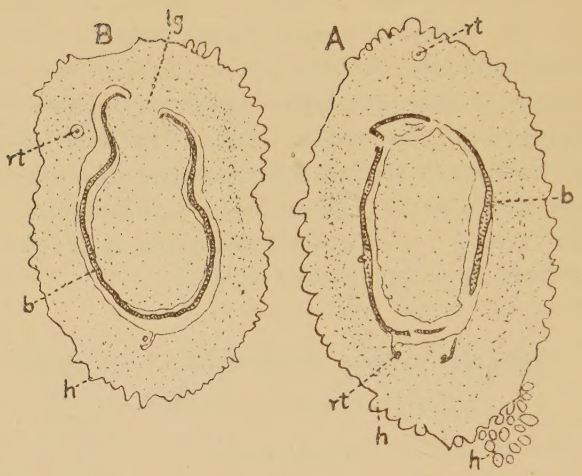
Material

This is incomplete specimens consisting of three cross sections, but as it has very peculiar hairs, it is worth while to describe here. These sections were formerly prepared, but as there was no exact record concerning them, the writer is not sure whether these three were cut from one specimen or from different specimens, but judging from the different size, they seem to be from different materials. For the sake of convenience they will be named Nos. A, B and C.

Specimen No. A. Largest, elliptical in cross section, 6×11 mm. in diameter (Text-fig. 5 A). The stele is also elliptical, $2{,}5 \times 5$ mm. in diameter and continuous though slightly damaged. In the cortex very distinct root traces are seen.

Specimen No. B. Middle-sized, elliptical in cross section, 5×8 mm. in diameter (Fig. 5; Text-fig. 5 B). The stele is horseshoe-shaped, $2 \times 4{,}5$ mm. in diameter, one part being interrupted by fundamental tissue, and has slight lateral depression.

Specimen No. C. Smallest, elliptical in cross section, 4×7 mm. in diameter, on one side with a root detaching. The stele is elliptical, 2×4 mm. in diameter. Separated a little from the main body is another



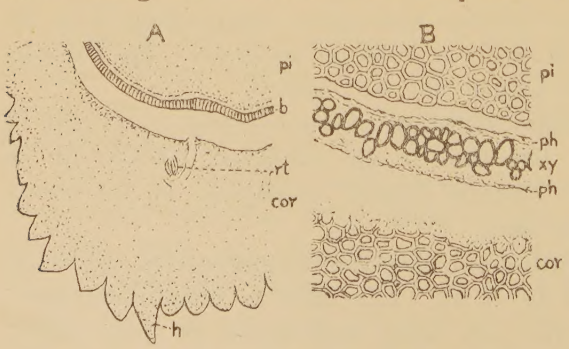
Text-fig. 5. Cross sections of Specimens No. A (A) and No. B (B), showing the solenostelic construction, in B interrupted by one leaf gap. Compare Pl. XVIII, Fig. 5. (× 6)
b, vascular bundle; rt, root trace; lg, leaf gap; h, hair

small fragment, perhaps a branch or leaf stalk, whose stele is not distinct.

All from Yubari, Ishikari, Hokkaido; Upper Cretaceous; found by Prof. K. Fujii in 1911 and prepared by him.

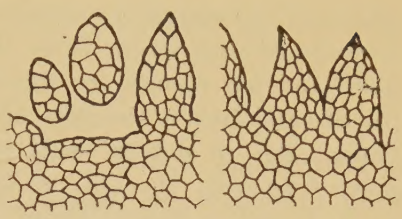
Internal Structure

On the periphery there are conical hairs (Text-fig. 6 A), and we can distinguish the cortex in two parts. The outer cortex consists of thin-walled and large-sized cells and its outer part passes to the hairs which are borne on the surface so closely as their bases connect with each other leaving no space for epidermal layer. These hairs are usually conical in section consisting of several large parenchymatous cells, usually 2–4 cells in breadth and 4–8 cells in length (Fig. 6;



Text-fig. 6. Cross sections of Specimen No. B magnified. A, one part of Text-fig. 5 B (lower part). Compare Pl. XVIII, Fig. 7; B, one part of A, showing the structure of vascular bundle. (A, × 15; B, × 50)
b, vascular bundle; xy, xylem; ph, phloem; pi, pith; cor, cortex; rt, root trace; h, hair

Text-fig. 7). The outer cortex passes inwards to the inner cortex which occupies the most part of the cortex consisting of thick-walled cells (Text-fig. 6 B).



Text-fig. 7. Cross section of the external part of the cortex, showing the structure of hairs. Compare Pl. XVIII, Fig. 6. (× 50)

The stele is solenostelic, consisting of a continuous ring in No. A and No. C, and in No. B it is interrupted in one place which will be a leaf gap (Text-fig. 5 B). The outline of the stelar ring is not smooth owing to the bad preservation. The vascular bundle is bicollateral (Fig. 7; Text-fig. 6 B); the xylem consists of tracheids, whose scalariform pitting is often seen, usually one to three, sometimes more cells thick. The protoxylem is exarch which can be distinguished, though it is not rather distinct, by smaller tracheids. The phloem is not preserved, its nature being uncertain, but separated a little from the tracheidal row is sometimes found a dark band of condensed cells which seems to represent the protophloem layer. Between this layer and the thick-walled cells of the inner cortex or of the pith is a parenchymatous layer, whose preservation is also bad showing no definite endodermal layer, so that we cannot decide whether this layer consists only of pericycle or of pericycle and a few layer of the cortex or of the pith.

The pith occupies the central part consisting of thick-walled cells just like the inner cortex, though their walls are somewhat thicker than those of the latter (Text-fig. 6 B). Within the cells of the cortex and pith we find numerous small granules showing the appearance of starch grains.

The root trace is embedded in the cortical tissue in all sides of the stelar ring, and its cortex is distinguished from the stem cortex by smaller cells, though there is no definite boundary between them. Its stele is not well preserved.

Affinity

It is very clear from its structure that this fossil plant belongs to the fern, and it is naturally considered to be the stem or rhizome as the root traces are found in the cortex. The most important characteristics of this fern are in its possessing a solenostele and multicellular hairs. The fossil fern with a solenostele was discussed by Miss Kershaw (5),

and it will be necessary to compare the present species with her species, *Solenostelopteris japonica*, from the same locality of Hokkaido. This plant and her species are similar in general:— the whole appearance, the size and form of the stele, and the construction of the fundamental tissue. But in details, both are different in some points:— in the present species, the size of fundamental tissue cells is larger, no parenchymatous layer is found within the sclerenchyma of the pith and cortex, no specially thickened portion of the tracheidal ring is found at the margin of the leaf gap, the root traces are found all round the stelar ring, and the tracheidal layer of the stetar ring is thicker. The most regrettable point in the description of her species lies in the absence of the outer cortex, which makes difficult to compare it with the present species whose outer cortex is well preserved, even showing the characteristic hairs. Considering from the internal structure, it will be natural to regard the present species to be nearly allied to, but rather different from her species.

Kershaw considered her species to be comparable with the species of Davallieae. The conical multicellular hairs as found in the present fossil, however, are not found in the species of Davallieae, and are found in *Loxsoma* (Gwynne-Vaughan 4, Bower 2) and *Dipteris* (Seward and Dale 11) whose steles are solenostelic. *Dipteris* differs from the present species in its having the mesarch protoxylem in the stem stele and thin-walled fundamental tissue cells. Though *Loxsoma* differs from the present fossil in its possessing the cortex consisting of thick-walled cells including some isolated parenchymatous islets, this fossil will stand close with this genus rather than others. Though the relationship between the present species and Kershaw's is not certain, the writer should include this species in her genus *Solenostelopteris* in its having the "vascular system of a solenostele", which is her diagnosis for the genus, while the specific name is derived from the allied genus *Loxsoma*.

Cycadeoidea petiolata, sp. nov.

Pl. XIX, Figs. 8–10; Text-figs. 8–9

Diagnosis

Cycadean petiole with no superficial appendages, rhomboidal in cross section. A thick cork layer on the periphery. Vascular bundles, more than thirty in number, arranged in a complex irregular form, each bundle collateral, mainly secondary; centripetal xylem none or

uncertain. In fundamental tissue no secretory tissue, but abundant thick-walled cells scattered.

Material

This is a rod-shaped piece, about 6 cm. in length, embedded in a nodule. It has a form of tetragonal cylinder, rhomboidal in cross section (Fig. 8; Text-fig. 8). Dark-brown in colour. Nine serial cross sections were made.

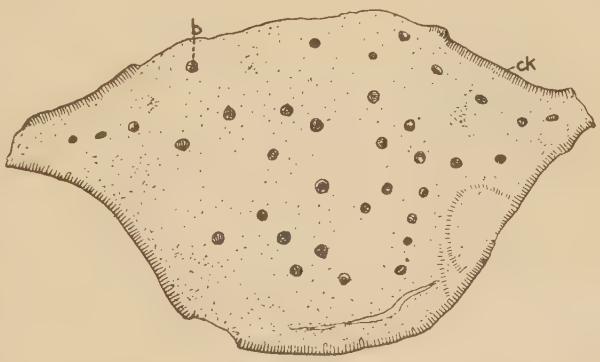
From Yubari, Ishikari, Hokkaido; Upper Cretaceous; found by Prof. K. Fujii in 1911 and prepared by him.

Internal Structure

The shape in cross section is rhomboidal, 19 mm. in long lateral diameter and 13 mm. in short horizontal diameter, each corner being somewhat damaged (Fig. 8; Text-fig. 8). Both lateral corners taper gradually, while both upper and lower ones are rather round though the upper side is somewhat damaged.

All round the periphery is a thin layer of cork tissue and the whole inner part is occupied by fundamental tissue, in which vascular bundles are scattered. On the lateral side is a band of cork tissue penetrating somewhat into the fundamental tissue which must have been caused by damage.

The arrangement of vascular bundles is so irregular that we cannot trace at once the order of arrangement. In such a case it is usually possible and natural to trace them by means of the position of the protoxylem or by the direction of arrangement of vascular elements. In the present case we cannot trace them completely even by these methods, as some bundles are quite disorganised. The number of bundles is thirty six, of which about six-

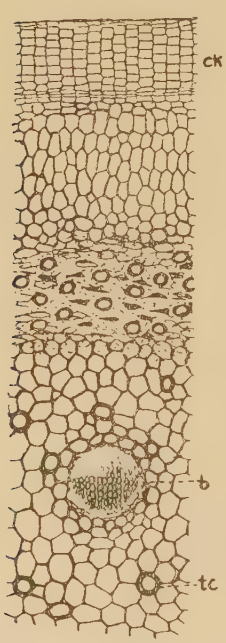


Text-fig. 8. Cross section of the petiole, showing the peripheral cork layer and the irregular arrangement of vascular bundles. Compare Pl. XIX, Fig. 8. (× 4)
ck, cork layer; b, vascular bundle

teen are arranged in periphery and the others are included, without definite order, within this peripheral ring (Fig. 8; Text-fig. 8). Some bundles show the rows of tracheids which point various directions (Fig. 10).

Histological Structure

The preservation of tissue is generally good except most of vascular bundles (Text-fig. 9). The external cork layer, about 1/2 mm. in thickness, consists of regular, radially arranged cells, ten or more cells thick (Fig. 9). Its outer surface is generally broken off exposing the cork cells, but in some parts we find, directly touching the cork cells, a layer of epidermal cells compressed or partly disorganised. Inside the cork layer is a layer of very flattened cells, one to three cells thick, and then a layer of somewhat larger, though flattened, cells, one or two thick; the former is a cork cambium and the latter a phelloderm. All these features show the epidermal or subepidermal origin of the cork[1]. Inside the cork tissue is a hypodermal layer consisting of thick-walled cells, somewhat radially elongated, which gradually passes into the ordinary parenchymatous tissue. In the parenchymatous fundamental tissue there are many thick-walled, generally somewhat smaller, cells scattered or in groups of two or three, and no secretory cavities are found.



Text-fig. 9. Cross section of the external part. Compare Pl. XIX, Figs. 9–10. (× 40)
ck, cork layer; b, vascular bundle; tc, thick-walled cell

The vascular bundles, separate from each other, are not well preserved, and no one shows a complete structure, being usually replaced by a black matter. They are collateral, consisting mostly of secondary elements (Fig. 10; Text-fig. 9). The phloem is generally disorganised, but in a few bundles it is seen that it consists of radially arranged elements, usually compressed severely. The xylem consists mostly of radially arranged tracheids traversed by some rows of medullary rays, and in the inside of each row are found small tracheids which represent the primary xylem. Opposite the primary xylem lies a tissue of two to four layers of thin-walled

1) Such a feature is found in *Cycadeoidea gigantea* (Seward 10).

parenchymatous cells, which then passes into the ordinary fundamental tissue. In this thin-walled parenchyma we find rarely a few indistinct cells with somewhat or very slightly thickened walls, which seem to represent the centripetal xylem. No special sheath is found on the periphery of the bundle.

Affinity

The general stature, size, form and the internal structure of the present fossil at once show it to be a Cycadean petiole. The arrangement of vascular bundles at the petiolar base of this group of plants is characteristic and complex, generally arranged in an inverted Ω-form in living Cycadales, and in a heart-shape in extinct Bennettitales, though sometimes very simple or irregular complex forms of arrangement are reported[1]. In the case of the present fossil, though the bundle arrangement is irregular and complex, we might consider it to be derived from a heart-shaped type. The bundle itself in the petiole is also differently constructed in living and extinct species; in the former the centripetal xylem is predominant, while in the latter the centrifugal xylem is predominant, the centripetal one being represented by a few tracheids. The present fossil shows the latter form, but the presence of centripetal xylem is very doubtful; even though it may be present it must be very rare. The absence of the centripetal xylem is also reported in some species of *Cycadeoidea*[2].

Considering these features it is sure that this fossil petiole might be that of *Cycadeoidea*, and it is interesting that the stems of *Cycadeoidea* were formerly found from the same province of Hokkaido:— *C. ezoana* Kryshtofovich (6) and *C. nipponica* Endo (3). But, the irregular arrangement of vascular bundles, absence or indistinctness of the centripetal xylem, the absence of secretory tissue, and the presence of thick-walled cells in the fundamental tissue are peculiar characters of this plant which cannot be found in other species hitherto known. It is even different from the two species from the same locality, and seems to be a new species, though the true nature of its stem is quite unknown. The writer, therefore, proposes to name it *Cycadeoidea petiolata*.

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1) In simpler cases the bundles are arranged in a series of a single ring:— *Cycadeoidea turrita*, *C. utopiensis*, *C. Wielandi* (Wieland 14), *C. micromyela* (Lignier 7), while in complex cases they are arranged very irregularly:— *Cycadeoidea ingens*, *Encephalartos Vroomi* (Wieland 13), *E. cycadifolius* (Matte 8).

2) *Cycadeoidea micromyela* has no centripetal xylem (Lignier 7).

Cycadeoidella japonica, gen. et sp. nov.

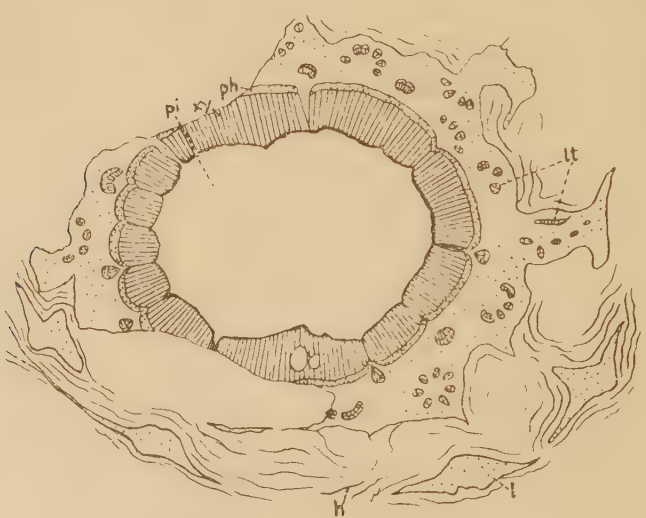
Pl. XIX, Figs. 11–14, Pl. XX, Figs. 15–19; Text-figs. 10–22

Diagnosis

Short slender Cycadean shoot; central axis with large pith clothed closely with spirally arranged, sessile, lanceolate leaves; all surfaces of leaves densely covered with long scaly hairs. Vascular bundles of the stem are of gymnospermous type; those of the leaf, 8–12 in number in each, derived from one leaf trace, are arranged in a ring, each with collateral structure consisting of secondary elements. Some tracheids of the stem bundle provided with bordered pits, one or two rows, but most of them with scalariform pits; those of the leaf bundle always have scalariform pits. Without definite centripetal xylem in both stem and leaves.

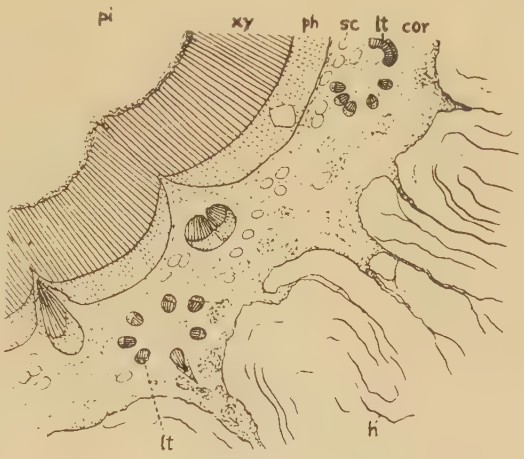
Material

Specimen No. A. A very good shoot including the summit, about 9 cm. in length and 5 cm. in diameter, surrounded with leaves covered with numerous scaly hairs; the whole embedded in a nodule. The central axis, 1,5 cm. in diameter, contains a large hollow pith



Text-fig. 10. Cross section of Specimen No. B, showing the central pith (cavity), the thick vascular ring, the cortex with leaf traces, and the scaly hairs outside. Compare Pl. XIX, Fig. 11. (× 2)
pi, pith; xy, xylem; ph, phloem; cor, cortex; lt, leaf trace; l, leaf; sc, secretory cavity; h, hair; lb, leaf bundle

cavity. At first, one cross section was made at the base, then cut longitudinally, and from one half ten longitudinal sections (Figs. 15–17; Text-figs. 12, 14, 16), and from the other thirty cross sections, both in succession, were made.



Text-fig. 11. One part of Text-fig. 10 (lower right side) magnified; various stages of the formation of leaf traces are to be seen. Compare Pl. XIX, Fig. 12. (× 5)

Specimen No. B. A fragment of another incomplete shoot with similar characteristics, somewhat thicker than No. A, 5 cm. or more in diameter. Two cross sections were made (Fig. 11; Text-fig. 10).

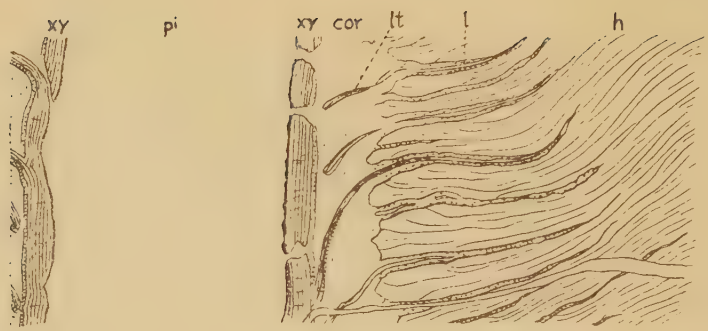
Both are embedded in the nodule, so that their structure must be traced from successive sections, longitudinal as well as transverse. The stem axis is clothed with leaves, sessile and lanceolate, about 12 mm. in breath and 15 mm. in length. One of the most prominent features of the leaf is the occurrence of plenty of long scaly hairs, which cover very closely all its surface stretching beyond the leaf tips. The basal part of the leaf is attached to the stem horizontally or somewhat inclined, but its distal part gradually curves upwards, lower leaves overlapping the upper ones.

From Yubari, Ishikari, Hokkaido; Upper Cretaceous; found by Prof. K. Fujii in 1911 and prepared by him.

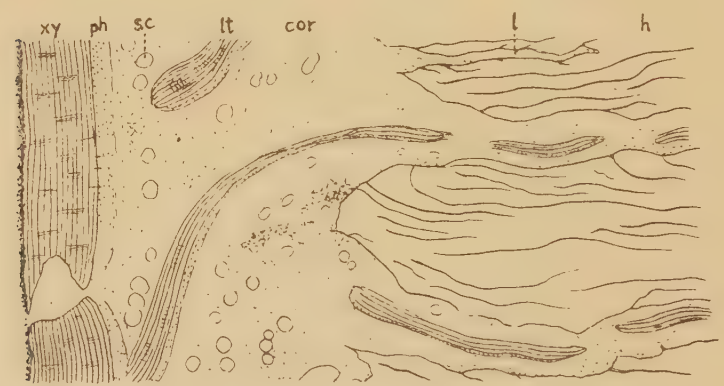
Internal Structure

From successive transverse and longitudinal sections we can see its internal structure. The following description is based mainly on longitudinal sections of No. A (Figs. 15–17; Text-figs. 12–17) and transverse sections of No. B (Fig. 11–12; Text-figs. 10–11).

The Stem. The central axis, 1,5–3 cm. in diameter, has a large pith, 1–1,5 cm. in diameter, whose tissue is mostly lost leaving a cavity substituted by nodule material. Surrounding the pith is a thick zone



Text-fig. 12. Median longitudinal section of Specimen No. A, showing the large pith, the vascular bundle, the leaf traces, and the leaves with hairs. Compare Pl. XX, Fig. 15, in which the whole section is shown. Text-Figs. 12, 14 and 16 are the successive longitudinal sections of Specimen No. A. (× 3)
Explanations as in Text-fig. 10.

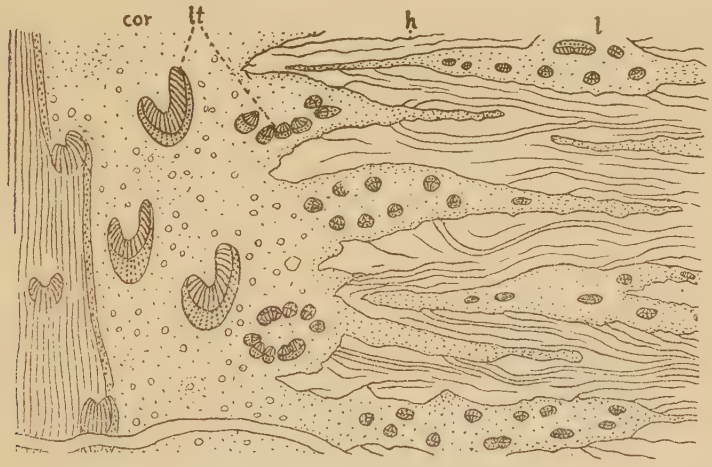


Text-fig. 13. One part of Text-fig. 12 magnified. Compare Pl. XIX, Fig. 14. (× 10)

of xylem traversed by leaf gaps, which in turn is surrounded by phloem and cortex, in which numerous leaf traces with peculiar arrangement are found (Text-fig. 10). As many leaves enclose the stem, the cortex connects with the tissue of the leaf bases. Numerous small cavities, secretory canals or sacs, traverse the cortical tissue.

The Leaf. The leaf has a slightly different structure in its different parts. The cross section of its basal part is rhomboidal, 6–8 mm. in lateral breadth and 3 mm. in longitudinal thickness, lateral edges somewhat elongated (Figs. 17–18; Text-figs. 16–17). In its central portion is a circular or elliptical ring of vascular bundles, separated from each other, eight to twelve in number (Fig. 19; Text-fig. 17). At the part not far from the base, the leaf shows a laterally elongated form

Text-fig. 14. Tangential section of Specimen No. A through the cortex, showing various stages of the formation of leaf traces. Compare Pl. XX, Fig. 16, in which the whole section is shown. Explanations as in Text-fig. 10. (× 3)



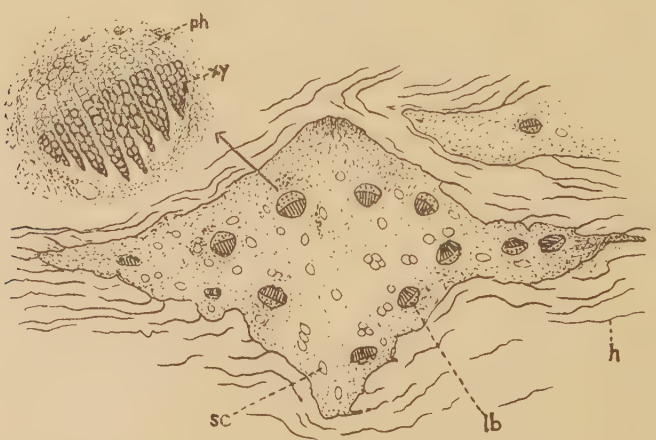
Text-fig. 15. One part of Text-fig. 14 magnified. (× 10)

in cross section, until at the middle part of the leaf it becomes flat, the lateral breadth reaching about 12 mm. and the thickness about 2 mm. The arrangement of vascular bundles is also influenced by this change of outer form; the ring flattens gradually in a lateral direction, until they are situated in two rows at the upper and lower sides of the leaf (Text-fig. 16; leaves at lateral side). All of the bundles are collateral, the xylem facing the inside of the leaf, thus showing the stem type rather than the leaf type (Text-fig. 17). Tracing still further toward the

tip, the leaf becomes thinner, and the tip is usually disorganised or broken into small pieces of indefinite structure.

Hairs on both sides of the leaf are scaly, attached parallel to the leaf surface overlapping with each other (Text-fig. 18). Each hair is very long, longer than the leaf itself, though its exact measurement is uncertain, and some hairs stretch beyond the leaf tip.

Text-fig. 16. Tangential section of Specimen No. A through the surface of the axis, showing the bases of detached leaves with vascular bundles circularly arranged. Between leaves numerous hairs are to be seen. Compare Pl. XX, Fig. 17, in which the whole section is shown. Explanations as in Text-fig. 10. (× 3)



Text-fig. 17. One part of Text-fig. 16 magnified, showing the basal part of the leaf in cross section. On the upper left side is shown one of the vascular bundles magnified. Compare Pl. XX, Figs. 18–19. (× 10)

The Leaf Trace. The mode of branching of leaf traces from the stem bundle is very clearly seen in transverse and longitudinal sections. In the first place, a part of the bundle of the stem is detached in a small mass which in tangential section of the axis is of heart- or arc-shape, open on the upper side, collateral in structure, the phloem embracing the lower side (Text-figs. 14–15). Further from the stem bundle, the detached trace gradually flattens and increases its curvature in a thin arc-form, open above, and then both ends approach each other at the upper median part; but meanwhile the arc is divided by radial rays

Text-fig. 18. One part of Text-fig. 12, showing the longitudinal section of the leaves, from both sides of which hairs are detached, overlapping each other. lb, leaf bundle; h, hair (× 8)

into separate pieces (Text-figs. 10–11, 14–15). This tendency becomes more and more prominent, until in the external cortex, several separate traces, eight to twelve in number, are arranged in a ring (Text-figs. 10–11); this is the condition of traces found at the leaf base.

Histological Structure

The preservation of parenchyma is generally bad though it is not very difficult to see its general structure. The other tissue, especially the vascular bundle, is well preserved.

The Stem. As the surface of the stem is covered with leaf bases, the epidermis of the stem is hardly recognised; in some parts where the leaf is not present, a cork layer is found fairly well developed. The cortex is composed of parenchyma with thin walls, in which many cavities, secretory (perhaps resinous or mucilaginous) canals or sacs, are found (Text-fig. 11); whether

Text-fig. 19. Longitudinal section of the xylem of the stem axis, showing the tracheids with various forms of membrane sculpture. (× 80)

they are canals or sacs is uncertain, but it seems to be sacs as they are also circular in longitudinal section (Text-fig. 13). On the periphery of the cavity no definite epithelial layer is found. The bundle is of coniferous type (Fig. 12; Text-fig. 11); the xylem consists of regularly arranged secondary tracheids traversed by medullary rays, usually one cell broad and one to twenty cells high. The structure of the tracheidal wall is hardly seen; it has certainly scalariform pits on all sides, but sometimes shows bordered pits, in one to three rows, either opposite or alternate, and occasionally we find the intermediate type between scalariform and bordered pits (Text-fig. 19). The wall sculpture of the ray cell, square or somewhat elongated in radial direction, is not clear. The phloem is relatively well preserved, being of the normal coniferous type, traversed by phloem rays, but the wall structure is uncertain. The pith, though the greater part has been lost, consists of large parenchymatous cells including some cavities, perhaps secretory ones.

The Leaf. The preservation of the leaf is generally bad. The epidermis connects with scaly hairs, one cell thick, like fern scales; the cross section of the hair mass agrees with that of ramenta of *Cycadeoidea*, but is far broader (Fig. 13; Text-fig. 20). Under the epidermis are found, though not constantly, one or two layers of small cells, with unthickened walls representing the hypoder-

Text-fig. 20. Cross section of hair groups, showing the flat scaly nature, one cell thick. Compare Pl. XIX, Fig. 13. (× 80)

Text-fig. 21. Stoma on the surface of a leaf. (× 80)

Text-fig. 22. Longitudinal section through the vascular bundle of the leaf, showing the scalariform tracheids. (× 80)

mis. We see sometimes stomata of the normal type (Text-fig. 21). The mesophyll consists of large parenchymatous cells including numerous

secretory cavities as in the stem. The vascular bundle, circular or elliptical in cross section, is collateral consisting of the same elements as those of the stem (Text-fig. 17). All of the tracheids, however, seem to be scalariform (Text-fig. 22).

Affinity

This fossil shoot has the general character of a Conifer in appearance, but in its essential points differs considerably from it. This plant shows many peculiar characters in having (1) the leaf bundles arranged in a ring, (2) the tracheids with scalariform pitting, (3) the large pith, and (4) plenty of long scaly hairs; these points will be shortly discussed below.

(1) Arrangement of leaf bundles. The arrangement of leaf bundles in a ring or in two rows inversely oriented is quite unfamiliar in Conifers, but is the form sometimes found in petioles of many ferns, Cycads, Bennettitales and some Dicotyledons and also of Monocotyledons. The foliage or foliage-like organs with such a bundle arrangement are, however, relatively seldom found in phylloclades of various kinds, cone scales of Conifers, and unifacial leaves of Monocotyledons. The arrangement of bundles of the leaves of this plant, therefore, must be one of the peculiar characters. (2) Pitting of tracheids. The scalariform pitting of tracheidal elements is characteristic in Pteridophytes, contrary to the bordered pitting of Gymnosperms. The distribution of two types of pitting, however, is not absolute, and in most of Gymnosperms, especially evident in primitive ones, a gradual transition from the scalariform pits to the bordered ones will be seen in the primary wood near the pith, in some cases scalariform pitting predominating in most part of the xylem[1]. The present fossil is very interesting as its tracheids, though mostly scalariform, sometimes show bordered pits or intermediate forms of these two kinds of pitting in some parts of the stem; such feature are also found in *Cycadeoidea* (Wieland 14). (3) Large pith. The large pith, more than 2 cm. in diameter, is characteristic in Cycads, Bennettitales and some Cordaitales among Gymnosperms. In this point the present fossil should show some affinities with these groups. (4) Scaly hairs. The presence of scaly hairs is rare in Gymnosperms but is characteristic in most of Pteridophytes. Among Gymnosperms, Bennettitales have such hairs,

1) Such is the case in *Stangeria* and *Cyadeoidea* (Wieland 14).

and in this point the present fossil is very similar to that plant group.

Considering these points, it is seen that the present fossil differs essentially from a Conifer, though having a general appearance of the latter. It has some similarities to Cordaitales in their general stature and large pith, but the present fossil has no characteristic primary xylem and its leaf is also different in structure. It has also some similarities to Cycadales and especially to Bennettitales with which it may stand in close relationship.

In the reproductive shoot of *Cycadeoidea*, or *Bennettites*, are found, surrounding the central axis, scaly leaves covered with long scaly hairs, while the vegetative axis, is surrounded by large petiolated leaves, though even the sterile part may be surrounded by scaly leaves just as in living Cycads. The arrangement of bundles at the petiole base of *Cycadeoidea* is complex and characteristic, though in the simplest case arranged in one ring[1], and the mode of departure of leaf traces from the stem axis is also complex and characteristic (Wieland 14). These features of *Cycadeoidea* are very similar to the present fossil, and its Cycadeoidean affinity will be naturally accepted. If this is truly the case, it may be either a young plant or a small bud. In the leaf bundle of this plant we cannot definitely show, owing to incomplete preservation, the presence of centripetal xylem, which is one of the characteristics of *Cycadeoidea*, though lacking in some species[2]. Moreover, this plant has a slender stature, broad scaly hairs, and only scaly leaves throughout, all these features suggesting differences from typical *Cycadeoidea*. The systematic position of this plant, of course, is not certain unless the other parts, especially the reproductive organs, are studied, but the general features, at least of the sterile shoot, suggest a Cycadeoidean affinity, especially to such a species as *Cycadeoidea micromyela*, which has, however, a larger size and longer petiolar base than the present fossil (Lignier 7). Thus, the present fossil must belong to a genus different from but related to *Cycadeoidea*; the generic name *Cycadeoidella* is derived from this well-known genus and the specific name from Japan.

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1) *Cycadeoidea micromyela* (Lignier 7); *C. turrita*, *C. utopiensis*, *C. Wielandi* (Wieland 14); *Bennettites maximus* (Stopes 12).

2) *Cycadeoidea micromyela* (Lignier 7).

Cunninghamiostrobus yubariensis, Stopes and Fujii

Pl. XXI, Figs. 20–26; Text-figs. 23–29

Stopes, M. C., and Fujii, K. (1910) Phil. Trans. Roy. Soc. Vol. 201, p. 45.

Dr. Stopes and Prof. Fujii described a coniferous branch clothed with scales, which was considered anatomically to be a coniferous cone though it had no seeds. Their material was incomplete and the characters in detail were left unknown. The diagnosis given by the authors is as follows:—

> *Cunninghamiostrobus*, gen. nov. Cone scales and axis in anatomical essentials like those of the living genus *Cunninghamia*.
>
> *C. yubariensis*, sp. nov. Cone intermediate in size between *Cunninghamia sinensis* and *C. Konishii*. Scales less pointed than in the former. In general shape more like *C. sinensis* than *C. Konishii*. Vascular strand of the scale very large and ovular strand small. Large resin ducts constantly associated with the vascular strand. Hypoderm well preserved. Large isolated sclerenchymatous cell, few in number. Upper Cretaceous, from Hokkaido, Japan.

The present fossil from the same locality accords well with the above description, and may represent the same species. But the writer's specimen being rather complete, even showing the seeds, he is able to add some new observations.

Diagnosis Modified

Coniferous shoot covered closely with cone scales. The axis is of a coniferous type; tracheids have bordered pits on their radial walls, one or two rows, opposite. The scale is separate, 15 mm. in length and 8 mm. in breadth; vascular bundles, ten or more in number, arranged in one row, collateral in structure; besides, two small (ovular) bundles with inverted orientation at the median upper side of the basal region; all these bundles derived from a large scale trace. Resin ducts distinct in both stem and scales. Between the scales near the top of the shoot are sac-like bodies representing seeds.

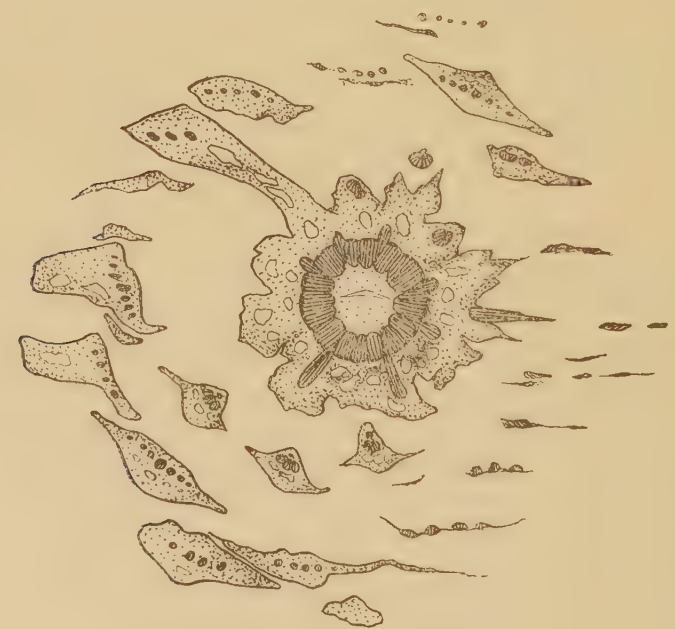
Material

Specimen No. A. A part of a shoot covered with spirally arranged scales, embedded in a nodule, the whole length being about 5 cm. and the breadth 2,5 cm. Eight serial cross sections (Fig. 20; Text-figs. 23–24) and seven longitudinal sections (Figs. 21–23; Text-figs. 25–28) were made.

Specimen No. B. A part of another shoot with similar aspect, though somewhat smaller. At the top several seeds are found between the scales. Two oblique sections were made (Fig. 25; Text-fig. 30).

As these two are embedded in nodules their exact form is not certain, and can only be reconstructed from the serial sections. Both are quite similar in general construction; in the center is a stem or cone axis with a diameter of 7–8 mm., on the periphery of which many leafy organs or cone scales are arranged spirally almost covering the stem surface. The scale is sessile, lanceolate or spatulate, 15 mm. in length and 7–8 mm. in breadth, and is attached to the stem surface almost perpendicularly or slightly inclined downwards. Thus, the general feature resembles a fertile shoot such as *Araucaria* rather than a close cone.

From Yubari, Ishikari, Hokkaido; Upper Cretaceous; found by Prof. K. Fujii in 1911, and prepared partly by him and partly by the writer.

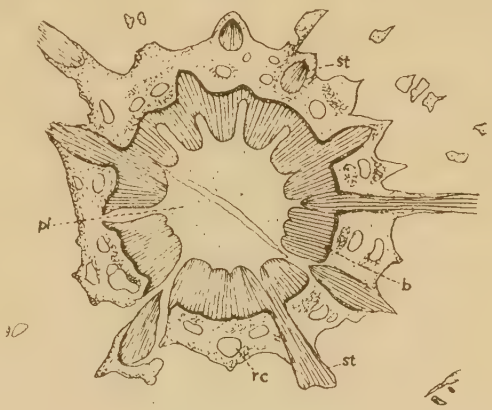


Text-fig. 23. Cross section of Specimen No. A, showing the general construction. In the center is the axis surrounded by cone scales whose bundles are shown. Compare Pl. XXI, Fig. 20. (× 3)

Internal Structure

From the successive transverse and longitudinal sections we can see the internal structure; the following description is based mainly on No. A.

The Axis. The axis, 7–8 mm. in diameter, is cylindrical, but as it is covered with scales we find in cross section irregular process of their bases on the surface (Fig. 20; Text-figs. 23–24). In the center is a large circular pith, 2,5 mm. in diameter, which is surrounded by a thick ring of vascluar bundle traversed by several scale gaps. The cortex encloses the vascular ring and is obliquely traversed by many scale traces detached from the vascular ring, and also there are many large resin canals (Text-figs. 23–24). As the scales are close together on the axis, the scale traces, about to detach themselves or already detached from the vascular ring, are numerous, so that the vascular ring is interrupted by many gaps.

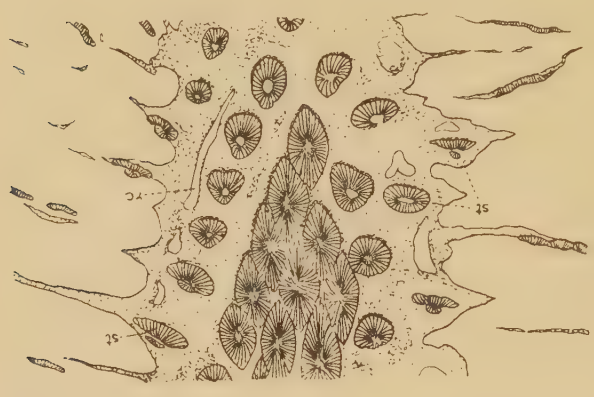


Text-fig. 24. The axis of Text-fig. 23 magnified. (× 6)
pi, pith; st, scale trace; rc, resin canal; s, scale; b, vascular bundle;

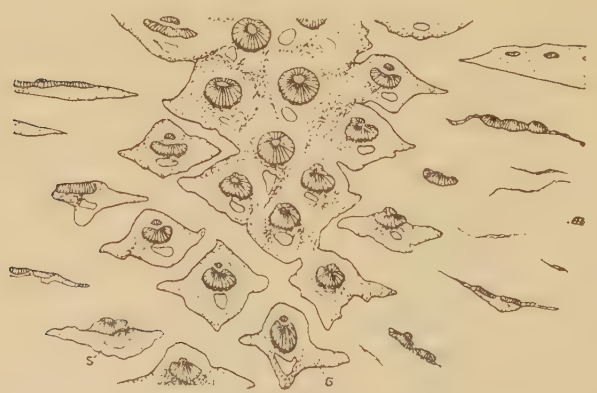
The Scale. The leafy organ or cone scale shows slightly different structure in its different regions, especially in its vascular bundles. The cross section of the basal part is rhomboidal, elongated laterally, 2 × 3 mm. (Figs. 23–24; Text-figs. 27–28); in its median upper side are a

Text-fig. 25. Median longitudinal section of Specimen No. A. Compare Pl. XXI, Fig. 21. Figs. 25–28 are the successive longitudinal (somewhat oblique) sections of Specimen No. A. Explanations as in Text-fig. 24. (× 6)

large bundle and a very small one with inverted orientation, both together forming an elliptical outline (Text-figs. 27, 29 A B); on the lower side of the large bundle three resin canals are arranged in a row, though only one or two are found owing to incompleteness of preservation. At the part somewhat distant from the base, the cross section is flat and the large bundle is divided into three, accompanied still by an inverted small bundle, which is itself divided into two (Fig. 24; Text-figs. 28, 29 B C); there are also three resin canals situated at the lower side of the three divided bundles. Traced further upwards (Text-figs. 28, 29 C D) the scale flattens more and more giving a breadth up to 7–8 mm. and a thickness of 2 mm.; its lateral edges taper gradually, or occasionally narrow suddenly into a ring-like process owing to the bad preservation. The three vascular bundles divide again gradually, until they number ten or more, which are arranged nearly in one row, the median one being largest and the lateral ones smaller; meanwhile, the small inversely orientated bundles degenerate gradually, and they are not found in the distal half



Text-fig. 26. Tangential section of Specimen No. A through the cortex, showing the scale traces just departed from the axis bundle. Explanations as in Text-fig. 24. (× 6)

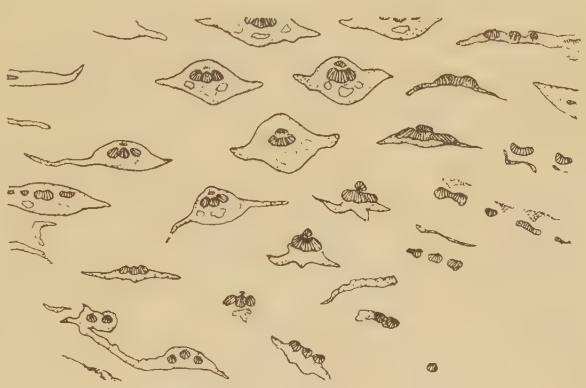


Text-fig. 27. Tangential section of Specimen No. A through the outer surface of the axis, showing the scale bases just departed from the axis; on the upper part they are not completely separated. Compare Pl. XXI, Fig. 22. Explanations as in Text-fig. 24. (× 6)

of the scale (Text-fig. 29 D). The small bundles with inverse orientation seem to supply to the seeds, and they were adequately called ovular strands by Stopes and Fujii.

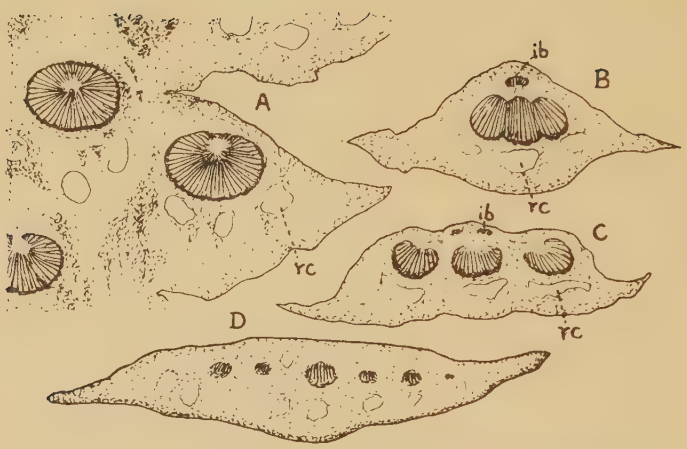
The distal part of the scale is badly preserved; usually only the bundles, arranged in one row, are found, fundamental tissue being decayed off (Text-fig. 28). Resin ducts which are very distinct at the basal region, three in number, become gradually indistinct at the middle region, and their termination is uncertain, though they divide within the scale as the bundles do.

The Scale Trace. It is very easy to trace the process of departure and the course of the scale trace, as many scales detach themselves regularly from the axis. The scale trace is a part of the vascular bundle of the axis bulged out and separated. When the trace is detached from the bundle ring a distinct scale gap is left on the latter which is gradually closed (Text-figs. 23–24). In tangential section of the axis the cross section of the trace will be given which is nearly fusiform containing a small pith in its center, surrounded by tracheids arranged radially (Text-figs. 26–27, 29 A). A little further out, the trace in cross section becomes flattened laterally; at the same time, the part of the bundle at the upper side is gradually reduced, at last only a small part remaining, which has naturally an inversely orientated structure (Text-figs 26–27); this is the form of the trace at the base of the scale as described above. Resin canals at the scale base are the direct continuation of those of the stem.

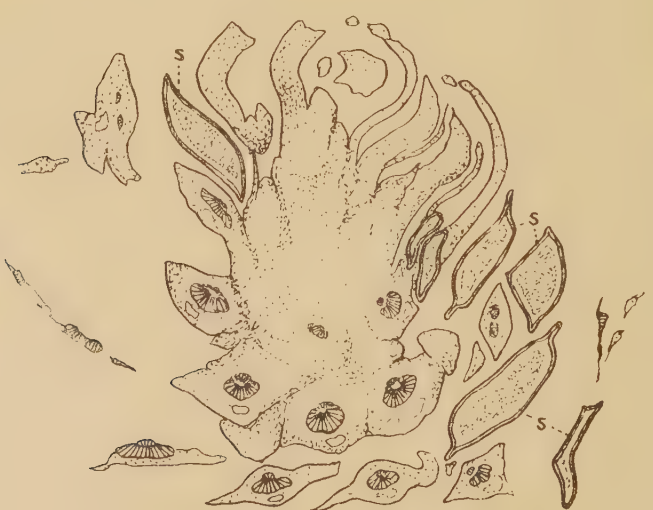


Text-fig. 28. Tangential section of Specimen No. A through the external part of the material, showing cross sections of scales. Compare Pl. XXI, Fig. 23. (× 6)
Explanations as in Text-fig. 24.

The Seeds. At the top of the shoot of No. B (Fig. 25; Text-fig. 30) and at a lateral part of the axis of No. A are found sac-like bodies, or the seeds, seven in number in one section of No. B, hidden between the scales. Their form is variable, perhaps owing to the compression;



Text-fig. 29. Cross sections of the scales at different parts, showing the mode of dividing of vascular bundles. A. Tangential section of the external part of the axis, where the scales are going to detach, showing the enclosed stage of scale trace in cross section. B. Base of the scale, showing one large three-lobed bundle and one small inversely orientated (ovular) bundle; compare Pl. XXI, Fig. 24. C. Somewhat distal rather than B, showing three large bundles and two small inverted (ovular) bundles. D. Middle part of the scale showing six bundles; inverted bundles are reduced and resin canals are divided. (× 20)
rc, resin canal; ib, inverted bundle



Text-fig. 30. Oblique tangential section of Specimen No. B through the cortex of the apical part, showing the seeds(s). Compare Pl. XXI, Fig. 25. (× 10)

the original form must have been a globular or ovoidal sac, 3 mm. in diameter and 1 mm. in thickness. They do not aggregate into a mass but occur isolated. The writer has never found any direct connection with the axis or scale notwithstanding that they are often in close contact, and though it is uncertain whether they belong to the axis or the scale, their position and structure suggest at once their seed nature. The sac usually contains only disorganised matter.

Histological Structure

The preservation of tissue is on the whole sufficiently good for a study of the histological structure.

The Axis. As the scales cover the axis its surface is mostly occupied by their bases. The surface is composed of epidermis and a few layers of hypodermis with slightly thickened walls. The cortex consists of large thin-walled parenchyma containing large resin canals, circular in cross section, though sometimes compressed; the surrounding cells are ordinary ones showing no peculiar thick-walled elements.

The vascular bundle is of normal coniferous type; the xylem consists mainly of secondary tracheids traversed by medullary rays, one or occasionally two cells broad and one to twelve or more cells high. The tracheidal wall is badly preserved and its structure is uncertain; often however, the tracheids show circular bordered pits on their radial walls arranged in one or two rows, in the latter case being opposite. The pitting of several tracheids near the pith, representing the protoxylem, is undoubtly scalariform, which passes gradually to bordered pitted form. The wall of the ray cell is also not well preserved, but we often see on its radial wall a large oval oblique pore, one on a cross field. The phloem is not clearly preserved, but it is certain that its elements are arranged radially like the xylem elements, as it is normally the case in Conifers.

The pith, well preserved, consists of homogeneous large parenchymatous cells including no other kinds of tissues.

The Scale. Among the epidermal layer composed of small cells, the outer wall of which is somewhat elevated, stomata are found on both sides of the scale. Each stoma is composed of two semilunar cells enclosing a shallow pore and is sunken somewhat below the epidermal layer like that of the normal coniferous leaf. The hopodermal layer, one or two cells thick, is found mainly on the lower side, and consists

of thick-walled elements. The fundamental tissue occupies the greater part of the scale and consists of large parenchymatous cells usually showing irregular outline owing to the bad preservation, in which resin canals having the same structure as those in the axis are found. Several thick-walled cells are found among the parenchyma scattered in all parts, though not very abundantly. The vascular bundle is of the same type as that of the stem, having no sheath. Some of the larger bundles are provided with groups of large cells on their lateral sides which seem, though not well preserved, to be transfusion tissue.

The Seed. The wall of the seed, or the integument, consists of several layers of small cells; the outer thin-walled layer, two or three cells thick, the middle stony cell layer, a single cell thick, and the inner fleshy layer, several cells thick. Its contents coagulate into an irregular structureless mass, but in some seeds where the contents have disappeared, thin walls are found separated from the integument.

Affinity

It seems clear that the present fossil has a coniferous affinity in the characteristic structure of the bundle both in the axis and scales, bordered pits on the tracheidal walls, transfusion tissue in some scale bundles, and stomata of the scale sunken below the epidermal surface. The very large bundle and the accompanying small inversely orientated bundle at the basal region of the scale are the most prominent feature which cannot be found in the coniferous leaves, and this is the main reason that Stopes and Fujii considered the leafy organ as the cone scale though they had never seen the seed attached to it, and they regarded the small bundle as ovular. In the present material we see the presence of sac-like bodies which undoubtedly represent the seeds, though their true connection with the scale is not seen. They are found not only on the apical part of the axis of No. B but also on the lateral side of No. A, and it seems natural to regard this fossil as a reproductive shoot, though most seeds had fallen off before fossilisation, as conjectured by Stopes and Fujii.

Since all the leafy organs, whether they bear seeds or not, show the same structure, including the inversely orientated bundles, they must be regarded as the cone scales, and consequently the central axis as the cone axis. This cone must be a fully ripened one as the scales open widely, some of which turning downwards. The inversely orientated bundles, or the ovular ones, found in all scales separate from the

main scale trace at the very base of the scale, and running through the upper side of the scale they gradually diminish in size and disappear at the middle of the scale. On the upper surface of the basal half of the scale where these bundles run through, we can find the epidermal layer showing no apparent trace of attachment of the seeds, but on the distal half of the scale where inverted bundles were no more seen, we could not descriminate any definite epidermis owing to the bad preservation. Thus, if the scale is actually of cone nature it will be natural to consider that the seed must have been attached at the middle or somewhat distal part of the scale where the inverted bundles are diminishing, these bundles supplying to the seed bases.

The number of seeds in each scale is not exactly known, but seems to be two considering the number of inverted bundles. The ligular processes on the upper side of the scale, which were interpreted by Stopes and Fujii as representing the ovuliferous scale, were not definitely shown in the present material, though such processes are not infrequently found all round the scale surface; they seem, however, to be due to accidents at the time of fossilisation.

Concerning the systematic position of this fossil the writer could not bring forward any fresh evidence, and therefore, follows the opinion of the original authors that its affinity is with the living genus *Cunninghamia*.

In conclusion, the writer wishes to express his sincere thanks to Professor K. Fujii for his helpful suggestions, and also for the specimens which he has generously put at the writer's disposal. Thanks are also due to the authorities of the British Museum (Natural History), who have kindly permitted the writer to make use of the valuable collection and the excellent library during his stay in London.

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Contents

Explanation of Plates XVIII–XXI

Pl. XVIII. Figs. 1–4. *Yezopteris polycycloides* Ogura
Figs. 5–7. *Solenostelopteris loxsomoides* Ogura

Fig. 1. Cross section of Specimen No. A, showing the central cavity and the arrangement of meristeles. Compare Text-fig. 1. (× 5)

Fig. 2. A part of Fig. 1 (upper right corner) magnified, showing the arrangement of meristeles. Compare Text-fig. 3. (× 12)

Fig. 3. Cross section of Specimen No. B, showing the arrangement of meristeles. Compare Text-fig. 2. (× 10)

Fig. 4. One of the small meristeles of Specimen No. A magnified; the row of tracheids, the protoxylem cavity and the thick-walled cells around the meristele are to be seen. Compare Text-fig. 4. (× 40)

Fig. 5. Cross section of Specimen No. B, showing a solenostelic vascular ring and irregular processes (hairs) on the periphery. Compare Text-fig. 5 B. (× 8)

Fig. 6. Cross section of the external part of the cortex magnified, showing the structure of hairs. Compare Text-fig. 7. (× 40)

Fig. 7. Cross section of a part of stelar ring. On the upper side is seen a part of the ring, and on the median lower part a root trace (somewhat indistinct in this figure). Compare Text-fig. 6. (× 40)

Pl. XIX. Figs. 8–10. *Cycadeoidea petiolata* Ogura
Figs. 11–14. *Cycadeoidella japonica* Ogura

Fig. 8. Cross section showing the irregular arrangement of vascular bundles. Compare Text-fig. 8. (× 6)

Fig. 9. Cross section of the peripheral region, showing the cork tissue. Compare Text-fig. 9. (× 40)

Fig. 10. Cross section of the central part showing two vascular bundles well preserved. The direction of the arrangement of tracheids of the two bundles are differently orientated. (× 40)

Fig. 11. Cross section of Specimen No. B, showing the large central pith, the thick vascular ring, and the cortex irregularly outlined. Compare Text-fig. 10. (× 1,5)

Fig. 12. A part of Fig. 11 magnified, showing the thick vascular ring, the cortex with leaf traces, and the fragments of hairs. Compare Text-fig. 11. (× 10)

Fig. 13. Cross section of hair groups, showing the scaly nature. Compare Text-fig. 20. (× 40)

Fig. 14. A part of Fig. 15 (Pl. XX) magnified, showing the cortex with leaf traces, and the leaves with hairs. Compare Text-fig. 13. (× 10)

Pl. XX. Figs. 15–19. *Cycadeoidella japonica* Ogura

Figs. 15–17 are successive longitudinal sections of Specimen No. A; Fig. 15 somewhat in larger scale than the other two.

Fig. 15. Median longitudinal section, showing the complete apical region with the central pith and peripheral leaves. Compare Text-fig. 12. (× 2)

Fig. 16. Tangential section through the cortex of the axis, showing the leaf traces in cross section. Compare Text-fig. 14. (× 1,5)

Fig. 17. Tangential section through the external part of the axis, showing the cross sections of leaves. Compare Text-fig. 16. (× 1,5)

Fig. 18. A part of Fig. 17 magnified, showing cross sections of leaves each with vascular bundles circularly arranged. Between leaves are seen cross sections of scaly hairs. Compare Text-fig. 17. (× 8)

Fig. 19. One of the leaves in cross section magnified, showing the circular arrangement of vascular bundles. Compare Text-fig. 17. (× 40)

Pl. XXI. *Cunninghamiostrobus yubariensis* Stopes and Fujii

Fig. 20. Cross section of Specimen No. A, showing the general structure. In the center is the axis, which is surrounded by scales. Compare Text-fig. 23. (× 4)

Figs. 21–23 are successive longitudinal (somewhat oblique) sections of Specimen No. A; Fig. 23 in larger scale than the other two.

Fig. 21. Median longitudinal section, showing the central pith and the peripheral cortex with scales attached. Compare Text-fig. 25. (× 4)

Fig. 22. Tangential section through the outer surface of the axis, showing the scales just departed from the axis. On the upper part they are not completely detached. Compare Text-fig. 27. (× 4)

Fig. 23. Tangential section through the external part of the material, showing cross sections of scales. Compare Text-fig. 28. (× 8)

Fig. 24. A part of Fig. 23 magnified, showing the cross section at the base of a scale. Three large bundles, a small bundle with inverted orientation on the upper side, and three resin canals are to be seen. Compare Text-fig. 29 B. (× 40)

Fig. 25. Oblique tangential section of Specimen No. B through the cortex of the apical region, showing the seeds. Compare Text-fig. 30. (× 8)

Fig. 26. A part of Fig. 25 magnified including three seeds. (× 40)

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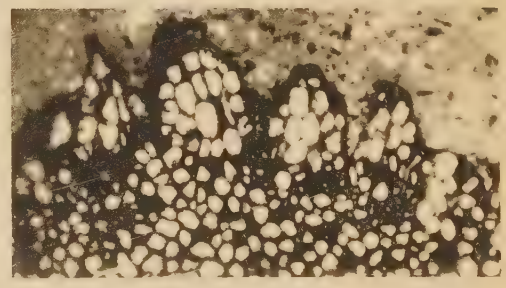

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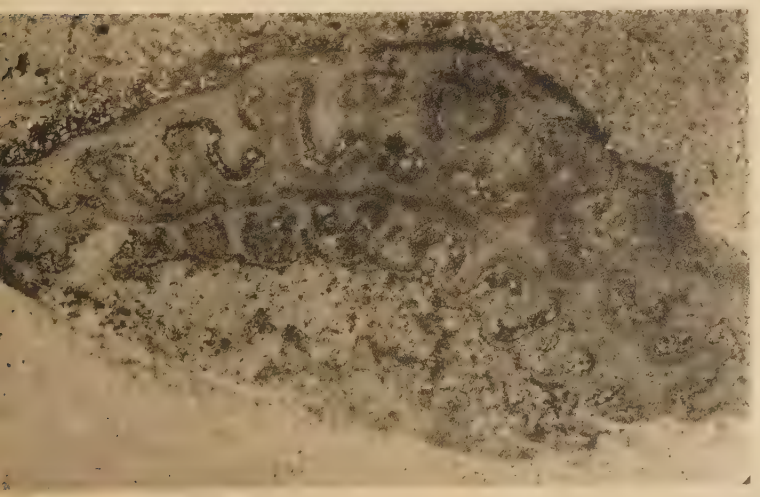

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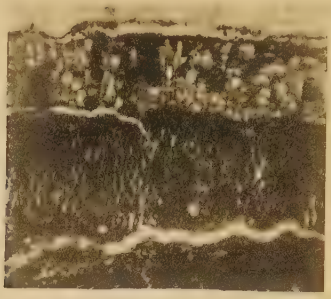

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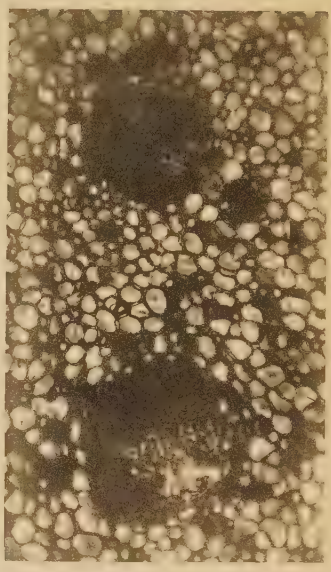

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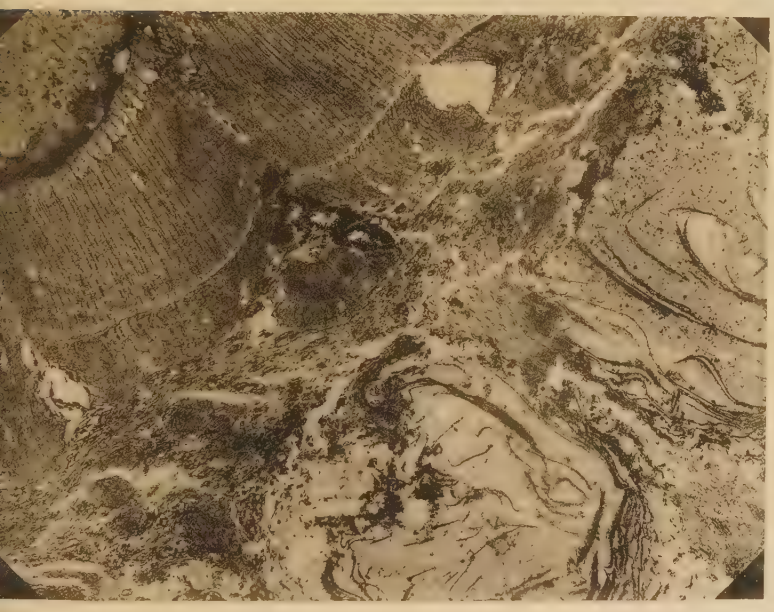

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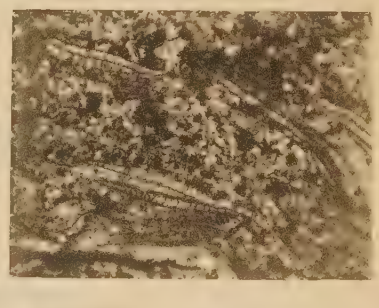
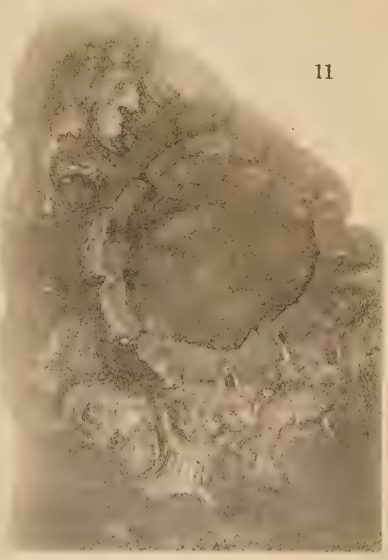
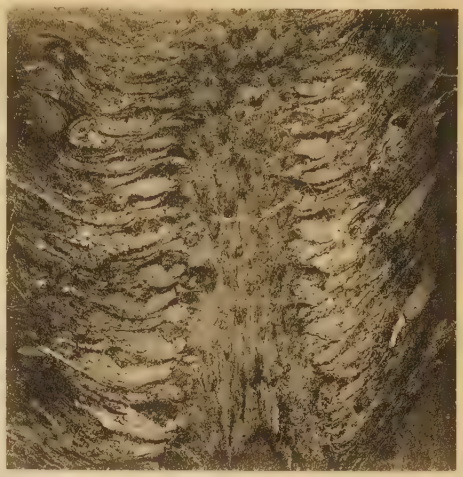


14

11



16



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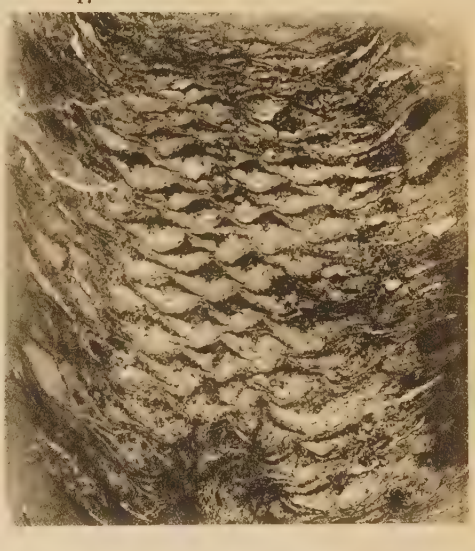

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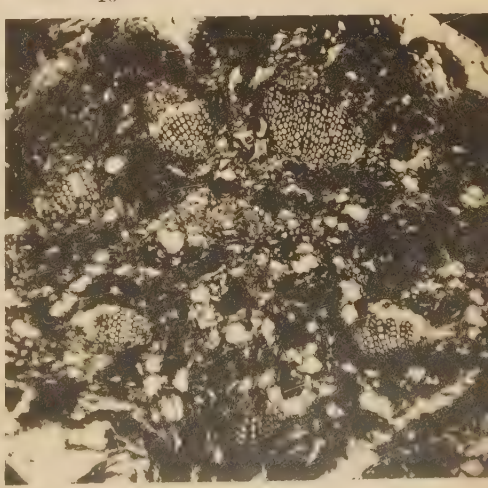
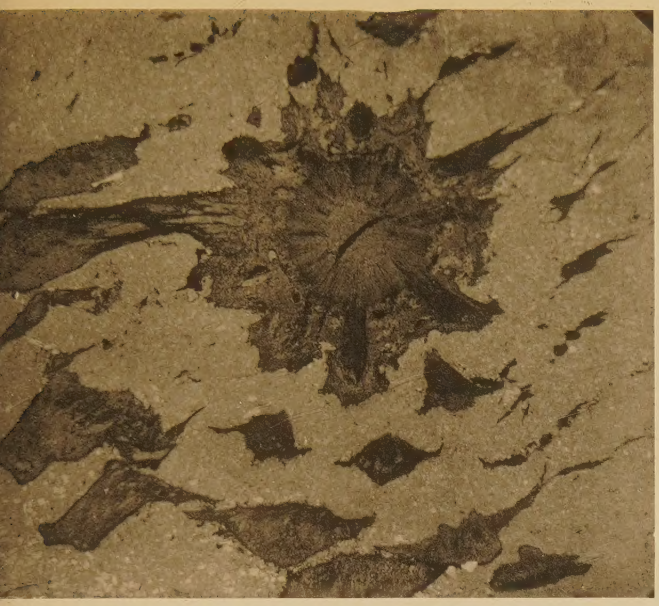




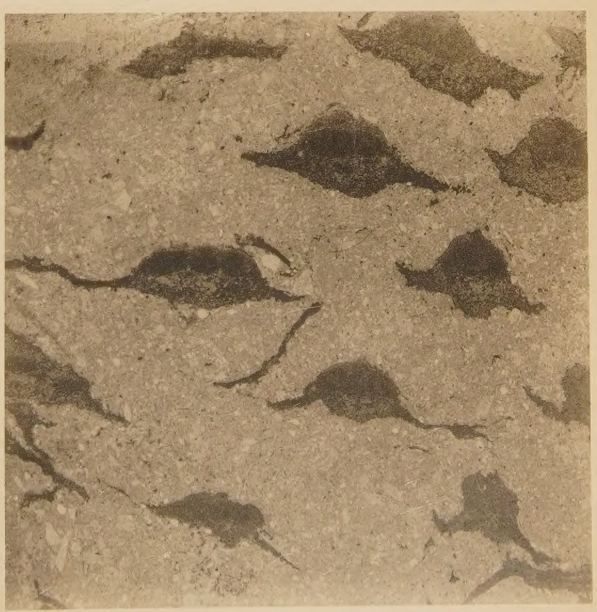
25

26

21

22

23



24

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